August 9, 1966

Dear Bill,

Under separate cover (two packages) I have sent to you a synopsis of the maize knob data that was discussed in our telephone conversation yesterday. By glancing through the maps you will get a feel for the distributions of the knob complexes even though much supporting data could not be included in these maps, such as the frequency of particular knobs in specific areas and their frequencies in specific races within an area. I realize that you will have questions that are not answered by the maps but could be answered by the raw data. When I visit you in October I will bring with me the raw data and also the individual tables that I prepared from them in order to be able to make the maps.

Longley and Kato did not record the knobs on each of the two homologues except in rare instances. This was done in my studies and also those of Kato and Blumenschein. In Mexico City last January, we were so pressed with organizing the data that I did not get the raw data from Kato for his recent studies of Tuxpeño nor such data from Blumenschein. Thus, their data are recorded on the maps for plants whereas those of mine and of Kato (from his Raleigh studies) are recorded for chromosomes.

The references to Teosinte knobs are taken from the diagrams of Longley and of Ting. The guesses of knob types in Arizona and New Mexico were made from the drawings in the 1938 paper of Longley. From Longley's data, there is little question that the maize of the Pima tribe had a different origin than that of the Navajo-Apache tribes.

Working up the data has been a tough job. Kato would do this rapidly and I certainly would let him do it in the future! I make too many mistakes and it takes too much time to find them and then correct my errors, either in the tables or the maps. Nevertheless, I felt that I should make an attempt to correlate the data. I am not now communicating my conclusions to Kato or to Blumenschein. I would prefer to have the conclusions made independently in order to compare modes of drawing conclusions.

Until later, then,

Best regards,

ORIGIN AND DISTRIBUTION OF KNOB COMPLEXES IN MAIZE

Analysis of the knobs in the chromosomes of present day maize indicates that there were at least four independent origins of maize and possibly a fifth. The wild ancestor of maize (teosinte ?) from which selections were made initially, grew in the region between the Central Mesa of Mexico and the northern part of Honduras. Each ancestor from which maize was obtained had a very distinctive knob constitution. The distinctiveness of each complex indicates some basic meaning of the complex in the evolution of the ancestor. This is evident in the nature of each complex. One complex had no knobs, another had only small knobs, a third had medium-sized knobs, and a fourth and possibly a fifth had large knobs (see diagrams). Through subsequent introgressions of one complex with another, and selections of viable or productive combinations of complexes, the initial significance of these complexes may have been lost or obscured. Nevertheless, the existence of such initial complexes is clearly evident in present day maize.

1. The no-knob complex. This complex is centered at the present time in the Central Mesa of Mexico and in the highlands of Guatemala. From examination of the knobs in the maize races in each of these areas it is possible to infer that the no-knob complex had its origin in the Central Mesa of Mexico and that an early introduction of this maize into the highlands of Guatemala is responsible for the distribution of this complex in the highlands. (See, however, discussion below.)

2. The small-knob complex. This complex originated in the highlands of Guatemala. Its influence is widespread due to migrations and to introductions into other areas.

3. The medium-knob complex. The exact place of origin of this complex is not clearly revealed by knob constitutions of present day maize. It is clear, nevertheless, that its influence is now confined largely to eastern Mexico, extending both north and south of the Campeche-Yucatan region. It has made a large contribution to maize of the Caribbean Islands and to the maize races of eastern South America.

4. The large-knob complexes. There may have been two independent origins of the large-knob complex. One complex has some knobs that are considerably larger than those of the other large-knob complex. The present center of the complex with very large knobs is now in Venezuela. It is present in maize of the coastal, inland and the mountain regions. Its influence has spread to the adjacent Caribbean Islands, particularly Trinidad and Tobago, Colombia, to the coastal and lowlands of Ecuador, and to the adjacent regions of Panama. Certain of its components appear in Zapalote. It may have originated in the Oaxaca-Chiapas region and been introduced early into Venezuela where it multiplied and spread. The other large-knob complex, some of whose knobs are not as large as those of the Venezuela complex, characterizes the maize of southern Guatemala and also that of southern and western Mexico. Its center of origin is not clearly evident but it may well have originated in the southern Guatemala-northern Honduras area. Its influence is extensive throughout Central America. It has been introduced into western South America but it has had very little influence on the maize of eastern South America. Although components of it are represented in the Caribbean Islands, its influence in the Islands is not as great as that of the Venezuelan complex, the medium-knob complex, the small-knob complex, and the no-knob complex.

Early Introductions of the Complexes into Distant Areas

1. One of the earliest introductions was that of the no-knob complex of the Central Mesa into the highlands of Guatemala where the small knob complex originated. Spread of the no-knob complex within this area lead to various strains carrying different components of each of these complexes. Following such intermixtures, maize from this area was introduced into western South America, 2, below.

2. A very early introduction of maize from the highlands of Guatemala into some part of western South America must have occurred. This maize had the "Andean complex." It was homozygous for a small knob in the long arm of chromosome 7 and was heterozygous for a tiny knob in the c position (nearest end of long arm) in chromosome 6. None of the other chromosomes had any knob. Because of the very extensive spread of this complex throughout western South America and subsequently into central and eastern South America, it is probable that this was the initial maize in all of South America and that it was propogated for a very long period of time before other maize was introduced into the e regions. The fact that all of this maize had the same knob constitution suggests that the initial introduction may have involved only a few kernels or that the initial selection for propogation came from a single plant.

(It is possible to consider that both the no-knob and the small-knob complexes originated in the highlands of Guatemala and that the no-knob complex, presently predominate in the Central Mesa of Mexico, was derived from an early introduction from the highlands of Guatemala. Because the density of the small-knob complex is low in the Central Mesa, it is probable that the knobs of this complex were introduced at a considerably later date after the no-knob complex had become well adapted in the Central Mesa and well distributed within this region.)

3. Maize from the highlands of Guatemala, possibly having only a small knob at the end of the short arm of chromosome 9, was introduced into the northern part of the United States. It gave rise to the Northern Flints of the U.S.

THE MIGRATIONS

1. The most extraordinary migration is that of the Andean complex following its early introduction into South America. It is now the predominate maize in the Andean Region, extending from Colombia into Chile. Much of this maize is not yet contaminated with maize that was introduced subsequently. It also spread eastward from the Andean regions into all of the parts of South America east of the Andes where this maize had been growing. It is now the predominant component of maize that is grown in central and eastern South America. The Andean complex is also a component of maize of the west coast of South America although diluted in most of the coastal regions by maize that has been introduced subsequently.

2. The small-knob complex spread south from the highlands of Guatemala into the highlands of Central America. Its northward spread was restricted as it is only weakly represent in the maize of Chiapas. The presence of components of this complex in western and northern Mexico may reflect migration from the Central Mesa of Mexico or from mixed races in Guatemala and Chiapas.

3. The medium-knob complex characterizes the maize of eastern Mexico where Tuxpeño is grown. Because Tuxpeño has been introduced into many parts of Mexico, the presence of components of this complex may be observed throughout Mexico, particularly in those races that are considered to be related to Tuxpeño. This complex extends southward into the Central American countries (see maps).

4. The Venezuelan large-knob complex has had a strong influence on maize of the adjacent Caribbean Islands, particulary in Trinidad and Tobago. It has spread into Colombia and into Ecuador, particularly along the coastal regions of Ecuador. It has also penetrated into Panama and components of it may be seen in other Central American countries although much diluted there. (For a special case of this, see maps of distribution of the large knob in the long arm of chromosome 9 in the Central American countries.) As stated earlier, this complex may have originated in southern Mexico or southern Guatemala and introduced subsequently into Venezuela. The Venezuelan complex appears in southern Bolivia in the race Perola (Arrocillo). It must have been introduced into Bolivia quite recently as components of it are absent or poorly represented in other races in the region of its introduction.

5. The other large-knob complex is now the predominant component of maize of much of Central America. In the highlands of these countries, the complex is mubh diluted by the no-knob, the small-knob, and the medium-knob complexes. This large-knob complex has spread into Yucatan and Campeche and also north into much of the maize of western Mexico. It has had a limited influence on the maize of the Central Mesa.

The Caribbean Islands

The maize of the Caribbean Islands is made up of a mixture of all of the complexes. In the northern islands, the no-knob, the small-knob, and the medium knob complexes predominate. This suggests that maize arrived in the islands quite late after much mixing of complexes had occured elsewhere. The eastern complex (medium-knobs) strongly influences the maize of the northern islands and it has had a marked influence on maize in the other islands. The large-knob complexes have had a lesser influence on maize of the

islands with the exception of the Venezuelan complex which is strongly represented in the maize of Trinidad and Tobago and to a lesser extent in some of the other islands (see maps). The maize of western Mexico has had very little influence on that of the islands.

The strong influence of the eastern (medium-knob) complex, evident in the islands, is also evident in eastern South America. The distribution of components of this complex to maize in central and eastern South America suggests that the complex was introduced into South America from the Caribbean Islands. In other words, the island maize is not derived from South America. Instead, the resemblance of maize from these two regions stems from introductions of maize from the islands into eastern South America. This introduced maize carried only some of the knobs of the medium-knob complex (see maps). This maize may have been introduced via the Rio Paraná, arriving in Paraguay by this route. This maize then introgressed with maize having the Andean complex that already was present in the area of introduction. Following introgression, the components of the medium-knob complex spread north and east and also, possibly, westward. The latter movement needs to be checked by additional studies.

The B-type Chromosome

The distribution of the B-type chromosome suggests that it was introduced into maize somewhere in Mexico. Its distribution in the northern hemisphere follows that of maize originating in Mexico. It is very poorly distributed in Central America, as the map will show. It is also poorly represented in the Islands and is almost absent in eastern South America. It was probably introduced into the Andean region with Canguil and Pisinkalla, both of which appear to be related to maize of west-central Mexico. Its presence in the lowlands of Chile may have come from introgressions with

Andean maize or from subsequent introductions into Chile. The distribution of the B-type chromosome is highly significant in interpreting the migrations and introductions of maize to the various areas of the hemisphere.

Abnormal chromosome-10

The distribution of Abnormal chromosome-10 is also significant for interpreting relationships of maize in the Americas. Its origin in Mexico seems evident. Its distribution in the northern hemisphere follows to a large extent that of the B-type chromosome.

Distribution of the Ga factor

A map is included showing the distribution of the Ga factors based on the information given by O.E.Nelson in the 1960 Maize News Letter. The distributions of ga are significant, especially for the relationship of maize in the highlands of Guatemala to that in western South America and in the corn belt of the U.S. Also, the presence of Ga^s in Pisinkalla is not unexpected.

Knobs with limited distributions and uncertain origins

Chromosome 1 long arm: Large, medium, and small knobs

" 2 short arm: Medium knob

" 3 short arm: Large, medium, and small knobs

" 4 short arm: Large, medium and small knobs

" 5 short arm: Large and medium knobs

" 6 a, b, and c knobs: Large

" 6 b, and c knobs: Medium

" 7 short arm: Medium knob

Some of these knobs have such limited distributions that their origins are obscured. I suspect that some of them, especially those in the short arms of chromosomes 2, 3, 4, and 5, and the long arm of chromosome 1 may have been introduced into maize from teosinte in recent times. Those in chromosomes 6 and 7 may represent poorly migrating types such as those of Arizona and New Mexico maize that did not migrate north and east.

RESTRICTED MIGRATIONS

Large-knob complex:	Chromosome 1 short arm
	Chromosome 2 short arm
	Chromosome 3 short arm
	Chromosome 5 short arm
	Chromosome 6 a, b, and c
	Chromosome 7 short arm
	Chromosome 9 long arm
Medium-knob complex:	Chromosome 1 short arm
	Chromosome 1 long arm
	Chromosome 2 short arm
	Chromosome 3 short arm
	Chromosome 4 short arm
	Chromosome 5 short arm
	Chromosome 6 b and c
Small-knob complex:	Chromosome 1 long arm
	Chromosome 2 short arm
	Chromosome 3 short arm
	Chromosome 4 short arm
	Chromosome 10 a knob
Odd knobs, restricted migrations:	Chromosome 1 long arm, Large knob
	Chromosome 4 short arm, Large knob
	Chromosome 6 a knob, Large, medium and small knobs

Knobs in Maize of Arizona and New Mexico.

Pima tribe:

Large knob	Medium knob	Small knob
Chromosome 2 long arm	Chromosome 2 short arm	Chromosome 1 short arm
" 3 " "	" 7 long "	" 5 long arm
" 4 " "		" 6 b + c
" 7 " "		" 7 short arm
" 8a (+b)		
" 9 short arm		

Navajo tribe:

Chromosome 1 short arm	Chromosome 2 short arm	Chromosome 5 long arm
" 1 long arm	" 6 a	" 6 a, b, c
" 2 " "		
" 3 short "		
" 3 long "		
" 4 short "		
" 4 long "		
" 7 " "		
" 8 a (+b)		
" 9 short arm		
" 9 long arm		
Abnormal chromosome-10		
B-type chromosome		

Non-migrating knobs:

Short and long arm of chromosome 1
Short arm of chromosome 3
Short arm of chromosome 4
Short arm of chromosome 7
Abnormal-10

Restricted migrations of knobs:

Long arm of chromosome 3
Long arm of chromosome 4
a knob in chromosome 6
Long arm of chromosome 7
Long arm of chromosome 9
Long arm of chromosome 8

Dilution of the Andean Complex by the Small-knob and Medium-knob Complexes in Central and Eastern South America.

Small-knob complex:

Chromosome 1 short arm
Chromosome 3 long arm
Chromosome 5 long arm
Chromosome 6 b
Chromosome 9 short arm
Chromosome 9 long arm

Medium-knob complex:

Chromosome 2 long arm
Chromosome 3 long arm
Chromosome 4 long arm
Chromosome 7 long arm
Chromosome 8 a (+ b)